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AUTHOR Kindfield, Ann C. H.
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ABSTRACT

The results of a study of the meiosis models utilized by individuals at varying levels of expertise while reasoning about the process of meiosis are presented. Based on these results, the issues of sources of misconceptions/difficulties and the construction of a sound understanding of meiosis are discussed. Five individuals from each of three levels of expertise in genetics participated in this study. The expert group consisted of one university professor, two visiting lecturers, and two advanced graduate students from the University of California Berkeley (UCB) Department of Genetics. The experienced novices were five senior undergraduate genetics honor students at UCB who had already completed their core genetics courses and who were concurrently working in genetics research. The inexperienced novices were five UCB undergraduate biology majors concurrently enrolled in an introductory genetics course. The five inexperienced novices had all scored above 87% on their first midterm exam and were interviewed following classroom exposure to meiosis. Three aspects of the participants' overall meiosis models--common correct features, misconceptions, and model qualities--are elaborated on. (32 references) (KR)

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Understanding a Basic Biological Process: Expert and Novice Models of Meiosis

Ann C. H. Kindfield
(formerly Ann C. Hildebrand)
McDonnell Postdoctoral Researcher
EMST
4533 Tolman Hall
UC Berkeley
Berkeley, CA 94720
annie86@violet.berkeley.edu

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Introduction

Mendelian genetics and the underlying process of meiosis have long been recognized as topics that are both crucial to understanding basic biology and often quite difficult for students to learn (Johnstone & Mahmoud, 1980; Finley, Stewart, & Yarroch, 1982). Because of the important and difficult nature of these topics, they have been the focus of a number of studies of expert and novice problem solving and of student conceptions in biology (Collins, 1986, 1989; Hackling & Lawrence, 1988; Hildebrand, 1985; Slack & Stewart, 1990; Smith, 1988). These studies have resulted primarily in the characterization of strategic knowledge applied to solving Mendelian genetics problems, the description/analysis of *isolated* student misconceptions about the related process of meiosis, and the recognition that students often do not make fundamental connections between Mendelian genetics and the process of meiosis. However, none of this work has included the systematic characterization of individuals' *overall* models of meiosis, research that could ideally provide insights into the sources of student misconceptions/difficulties and more generally into the nature of how individuals construct their understanding of processes crucial to a meaningful understanding of the biological world.

In this paper, I report on the results of a study of the meiosis models utilized by individuals at varying levels of expertise while reasoning about the process of meiosis. Based on these results, I address the issues of sources of misconceptions/difficulties and the construction of a sound understanding of meiosis. In general, individuals' meiosis models consist of their models of chromosomes (i.e., the participating entities) and their models of the process itself (i.e., the series of chromosome changes/movements that define the process). Stewart & Dale (1989), Stewart, Hafner, & Dale (1990) and Brown (1990) have recently reported on meiosis models utilized by high school students as have Thomas (1988) (cited in Brown, 1990) and Smith (1990) for college students. The work presented

here extends that reported by these authors through the inclusion of individuals ranging in expertise, from introductory college students to practicing geneticists, and more detailed microanalysis of the meiosis models exposed by these individuals in a novel reasoning situation. This work is one component of a larger study designed to elucidate the nature of conceptual understanding of subcellular biological processes and the role played by diagrams in that understanding (Hildebrand, 1989).

Methods

Five individuals from each of three levels of expertise in genetics participated in this research. The *expert* group consisted of one university professor, two visiting lecturers, and two advanced graduate students from the UC Berkeley Department of Genetics (3 females/2 males). The *experienced novices* were five senior undergraduate genetics honor students at UCB who had already completed their core genetics courses (with A averages) and who were concurrently working in genetics research laboratories on senior thesis projects (2 females/3 males). The *inexperienced novices* were five UCB undergraduate biology majors concurrently enrolled in an introductory genetics course (3 females/2 males). The five inexperienced novices had all scored above 87% on their first midterm exam and were interviewed following classroom exposure to meiosis.

Participants completed a 1.5-2 hour individual interview consisting of the following segments: (1) working on a non-traditional genetics problem in a combined think-aloud/clinical interview setting, (2) answering interviewer follow-up questions, and (3) identifying and discussing a series of standard diagrammatic representations of DNA, genes, and chromosomes. All interviews followed the same format except that inexperienced novices were also asked to diagrammatically represent a hypothetical cell going through meiosis at the end of segment (2).

More specifically, the segment (1) genetics problem, designed to require direct reasoning about the process of meiosis, consisted of a verbal description of a particular eukaryotic cell, three individually presented sets of gametes that could result from this cell going through meiosis (having increasingly complex solutions), and a request to describe the specific meiotic events that would lead to the formation of each gamete set. The cell description, request, and each gamete set were presented on individual 4 X 6 cards as shown in Figure 1. Some interviewer follow-up questions were routinely asked during segment (2) of each interview, but most follow-up questions were tailored to individual's behavior while working on the problem. The general intent of these questions was to have participants elaborate on biological concepts they mentioned and diagrams they drew while problem solving. Finally, during segment (3), participants were sequentially shown the 10 standard representations in Figure 2, each of which was printed on a 4 X 6 card. After identifying and discussing individual representations, each participant was asked to compare eight specific pairs (5&9, 5&2, 5&7, 5&6, 6&7, 4&6, 3&4, 3&7), focusing on the correspondence between components and size relationships.

All interviews were videotaped and the audio portions were transcribed. Videotapes, transcripts, and participant-generated diagrams served as the data analyzed for this study. These data were subjected to detailed microanalysis, that is, detailed qualitative analysis of individual behavior from which generalizations about components of reasoning and underlying understandings can be derived, which resulted in the characterization of individuals' overall meiosis models.

Results

Because the problem utilized in segment (1) of the interview required that participants reason about the process, rather than simply about the outcomes, of meiosis, their solutions to the problem were equivalent to their models of meiosis

Card 1

Suppose you have a diploid cell from a eukaryotic organism for which the haploid chromosome number is 2 (N=2). The organism is heterozygous for three different genes -- a, b, and c. The a and b genes are genetically linked, while the c gene is located on a different chromosome.

Card 2

Suppose that you can directly observe the genotypes of the four gametes that result when a **single diploid cell** undergoes meiosis. With respect to genes a, b, and c, what events would have to occur during the **specific** meiosis that gives rise to each of the sets of gametes on the following cards?

(NOTE: Each set of gametes is the result of a single diploid cell undergoing a single meiosis; 1's and 2's indicate the parental origin of each of the alleles.)

Card 3

i) $a_1b_1c_2$ $a_1b_1c_2$ $a_2b_2c_1$ $a_2b_2c_1$

Card 4

ii) $a_1b_1c_1$ $a_1b_1c_2$ $a_2b_2c_1$ $a_2b_2c_2$

Card 5

iii) $a_1b_1c_2$ $a_1b_2c_1$ $a_2b_1c_2$ $a_2b_2c_1$

Cards 4 and 5 were presented only after an individual had completed her/his work on the preceding gamete set.

Figure 1. The cell description and problem presented to each participant. Cards refer to individual 4 X 6 on which various pieces of information were presented.

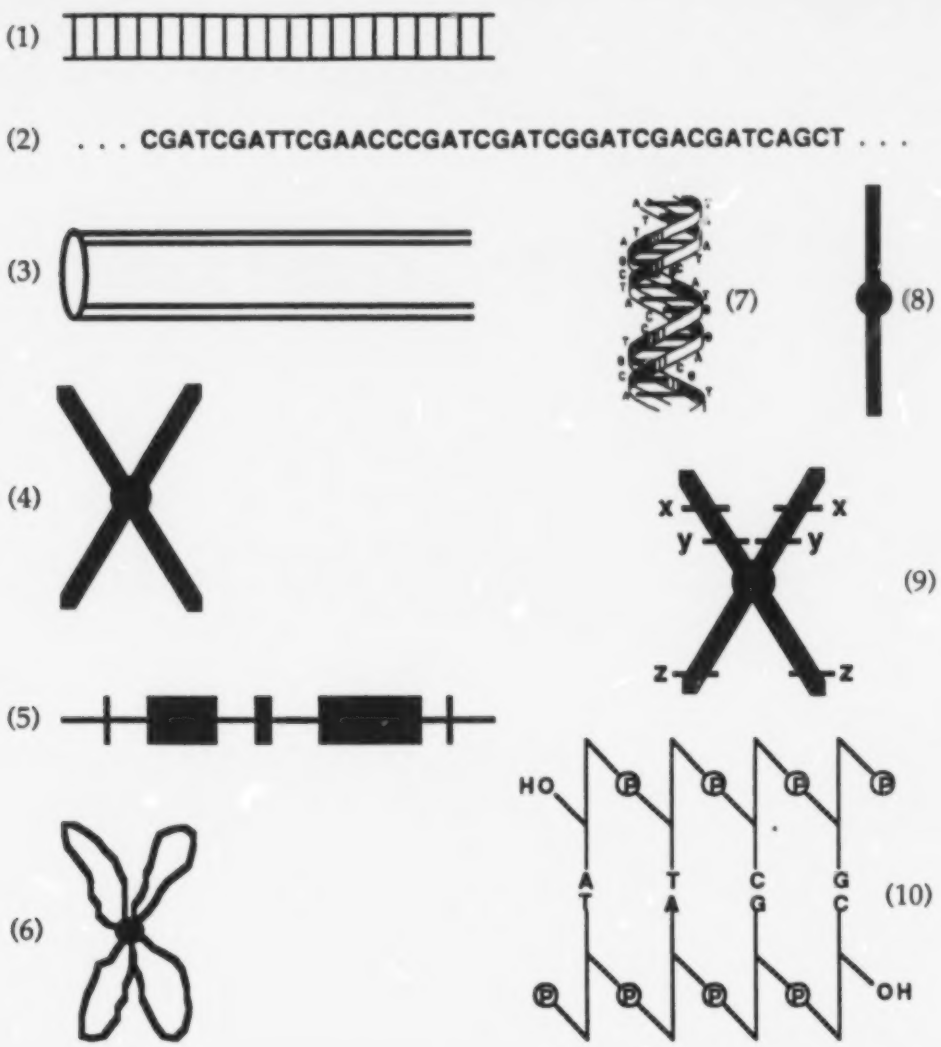


Figure 2. Standard representations (numbers adjacent to each representation indicate their order of presentation during the interview). (1) double-stranded DNA, (2) single-stranded DNA, (3) replicated chromosome, (4) replicated chromosome, (5) gene, (6) replicated chromosome, (7) DNA, (8) unreplicated chromosome, (9) replicated chromosome, (10) DNA.

(see Kindfield (1990) for a more detailed explanation). Thus, participants' chromosome and process models were derived from their problem solutions, supplemented by relevant information gleaned from interview segments (2) and (3).

All 15 participants revealed rather elaborate meiosis models. Two experts and 3 experienced novices exposed completely correct overall meiosis models, 3 experts and 1 experienced novice exposed correct chromosome models and slightly flawed process models, and the remaining participants (1 experienced and all 5 inexperienced novices) exposed flawed chromosome and process models. Each of the 10 alternate overall meiosis models was unique in terms of the particular combination of chromosome and/or process misconceptions underlying the flawed model. However, all 10 alternate models shared a set of correct model features, and certain component misconceptions were common to more than one alternate model, often according to level of expertise. Participants' meiosis models were also distinguishable in terms of three overall model qualities according to level of expertise. In the sections that follow, I elaborate on these three aspects of participants' overall meiosis models, that is, common correct features, misconceptions, and model qualities. These three sections are preceded by a brief review of meiosis.

Meiosis Review

Meiosis is the process by which two sets of chromosomes present in one initial cell nucleus (a nucleus defined as diploid) are ultimately distributed among four nuclei such that nuclei of each of the four product cells formed following cell division contains only one set of chromosomes (nuclei defined as haploid). In females, the product cells are eggs or ova, and in males, the product cells are sperm (for animals) or pollen (for plants). Thus, the product cells of meiosis are the sex

cells, pairs of which can fuse at fertilization initiating the production of offspring.[1] Meiosis-related concepts described in the following subsections are illustrated in Figure 3.

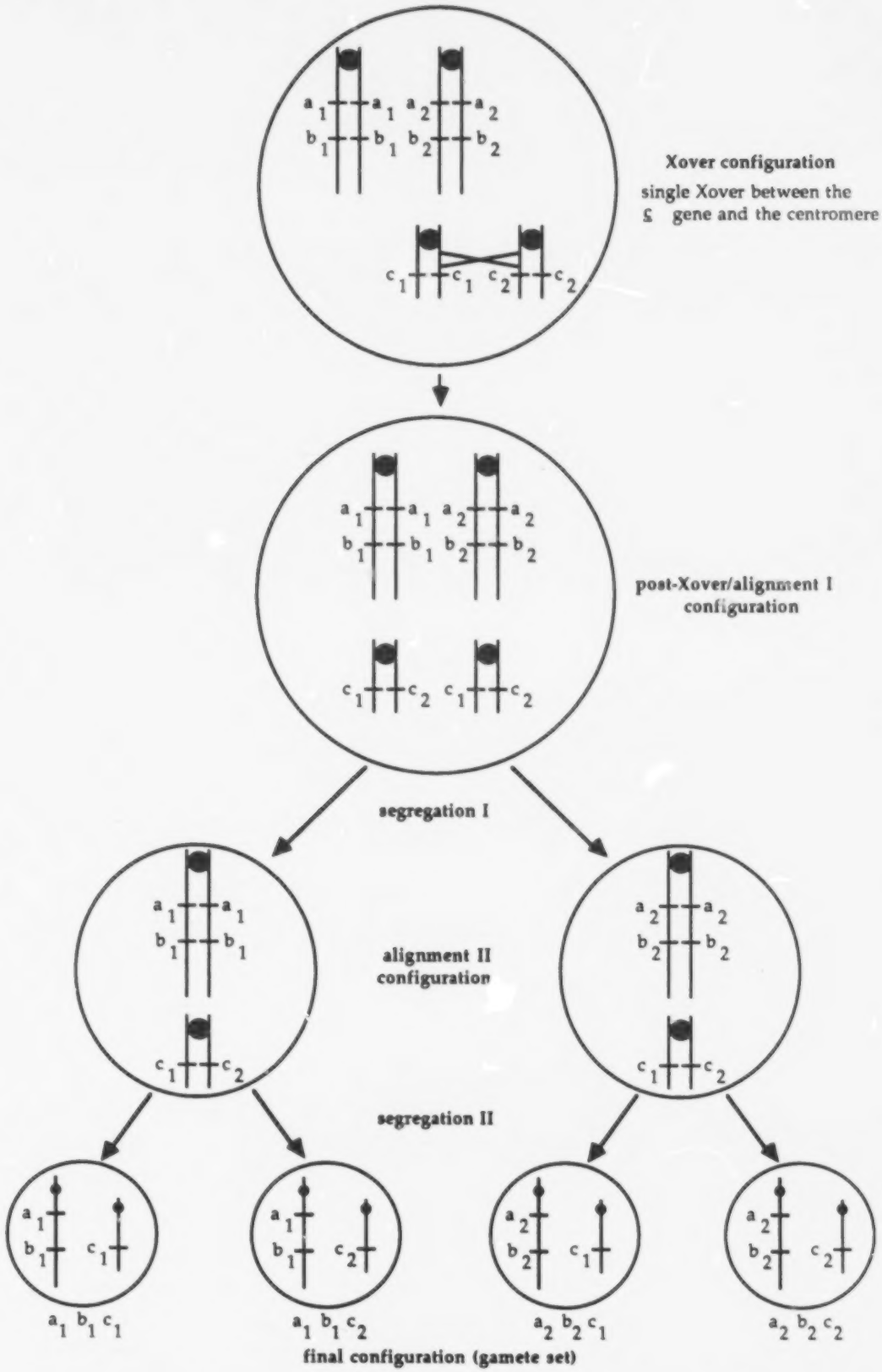
Ploidy

Turning first to chromosome number, each species of organism has a characteristic number of different chromosomes. Each different chromosome contains a subset of all the genes that are characteristic of that species. One set of all the different chromosomes constitutes the genetic make-up of that species. A cell nucleus that contains one set of all the different chromosomes for that species is said to be haploid or to contain the haploid number (N) of chromosomes. A cell nucleus that contains two sets of all the different chromosomes for that species is said to be diploid or to contain the diploid number (2N) of chromosomes. In essence, a diploid cell contains two 'copies' of each of the different chromosomes characteristic for that organism. In a diploid cell, the two 'copies' of a given chromosome are said to be homologous to one another and constitute a homologous pair of chromosomes. The two chromosomes of a homologous pair are 'copies' in the sense that they contain that same genes and the genes contained in each of those chromosomes are positioned at the same location along the length of each chromosome. Homologous chromosomes also have similar physical structures at the beginning of meiosis. However, they are not necessarily identical copies of one

[1] Certain organisms do maintain haploid (i.e., the one-set-of chromosomes) nuclei following meiosis as one (possibly the primary) component of their life cycle. Beyond contributing specifically to the formation of sex cells, meiosis more generally functions in the production of genetic variability through the reshuffling of specific versions of genes (alleles), that is, it serves as one of the two primary components of a sexual reproductive cycle. This variability is further enhanced when two haploid cell nuclei fuse to form a diploid (containing two sets of chromosomes) nucleus, the other primary component of a sexual reproductive cycle. Thus, though not necessarily transient (as are human eggs and sperm), meiotic products or their descendents ultimately function in sexual reproduction.

Figure 3. Illustration of some important aspects of meiosis. The meiosis shown here is one possible solution to gamete set (ii) (see Figure 1). Configuration refers to particular spatial arrangements of chromosomes at static points during meiosis. In the Xover (i.e., crossover) configuration, chromosomes are replicated (lines=chromatids and dots=centromeres), homologous chromosomes (i.e., chromosomes containing the same genes (e.g., a and b) though possibly different alleles (e.g., a_1 vs a_2) of those genes) are paired, and the X between the two c chromosomes indicates the position of the crossover event. In the post-Xover/alignment I configuration, homologous pairs are aligned and the effect of the crossover event is reflected by the exchanged c_1 and c_2 alleles in the c chromosome pair. In the alignment II configuration, individual chromosomes that separated as a result of segregation I are aligned in the center of each intermediate nucleus. In the final configuration, each final product nucleus contains one of each unreplicated chromosome as a result of segregation II. According to the more classical view of ploidy, the initial nucleus is diploid (2N), that is, it contains two sets of ab and c chromosomes. The final nuclei are haploid (N), that is, each contains one set of ab and c chromosomes. Ploidy is essentially undefined for the transient intermediate nuclei. (See Kindfield, in press, for a discussion of the classical vs modern view of how ploidy changes throughout the cell cycle.)

(Figure 3 continued on next page)


Xover configuration
single Xover between the
gene and the centromere
post-Xover/alignment I
configuration
segregation I
alignment II
configuration
segregation II
final configuration (gamete set)

another in the sense that the specific genetic information present for each of the genes (i.e., the specific alleles) along the length of each chromosome can vary.

Chromosome Structure

Before replication, each chromosome consists of a single double-helical DNA molecule containing single copies of all the unique genes[2] that make up that chromosome. When a chromosome replicates, the result is a chromosome consisting of two identical double-helical DNA molecules called 'sister chromatids' that are physically attached to one another at a point called the 'centromere'.[3] The consequence of this is that a replicated chromosome now contains two identical copies of each of the unique genes that make up that chromosome. Both unreplicated and replicated chromosomes are referred to simply as 'chromosomes'. When replication occurs, the number of chromosomes (discrete physical entities) present in the cell remains the same while the amount of DNA and the number of genes is doubled. Technically, the term 'chromatid' only refers to each of the subunits of a replicated chromosome. Calling an unreplicated chromosome a chromatid is an inaccurate/inappropriate use of the term 'chromatid'.

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[2] Unique genes are genes that occur once in the haploid genetic constitution of an organism. The genes a, b, and c are unique genes for the hypothetical organism in the meiosis problem in Figure 1.

[3] The DNA of both unreplicated and replicated chromosomes is associated with a variety of proteins, but the presence and functions of these proteins have no significant bearing on solving the meiosis problem in Figure 1. For this reason, the presence of these proteins will be disregarded throughout this paper.

The process of replication occurs once at a specific time during the cell cycle[4] preceding mitosis or meiosis and cell division.[5] Prior to replication, all chromosomes in a cell nucleus are unreplicated. Following replication, thus at the beginning of meiosis, all chromosomes in a cell nucleus are replicated. Following nuclear division, the resulting nuclei now contain unreplicated chromosomes until they reach the point in their individual cell cycles that DNA/chromosome replication occurs again. It is only during mitosis or meiosis, and thus after chromosomes are replicated, that they are condensed into forms that are visible as discrete entities under a light microscope.

Process Aspects of Meiosis

Two related components comprise the process aspects of meiosis: stages (meiosis I and meiosis II) and phases (prophase I, metaphase I, anaphase I, telophase I, prophase II, metaphase II, anaphase II, and telophase II (where Is and IIs refer to stages)).

Stages. In the first stage of meiosis, a single diploid nucleus divides into two nuclei (intermediate products of meiosis). During the second stage of meiosis, each of the nuclei produced as a result of meiosis I divides again resulting in the formation of a total of four haploid nuclei (final products of meiosis), two from each of the products of meiosis I.

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[4] 'cell cycle' refers to the growth cycle of a cell which includes five successive phases, G1-S-G2-M-C. The process of replication occurs during S phase and either mitosis or meiosis (both nuclear divisions) occurs during M phase just prior to cytokinesis or cell division that occurs during C phase. Thus, the processes of replication and meiosis are temporally separated by the G2 phase of the cell cycle. Although other processes that contribute to nuclear and cell division occur during G2, these processes are irrelevant to solving the meiosis problem in Figure 1, and therefore are not considered in this review of meiosis knowledge.

[5] Technically, mitosis and meiosis are nuclear divisions that may or may not be followed by cell division depending on particular species characteristics and cell type characteristics within particular species.

Phases. The process of meiosis consists of a series of systematic chromosome movements/interactions that ultimately result in the production of four haploid nuclei from a single diploid nucleus. Subprocesses or events characterized by particular spatial arrangements of chromosomes and/or specific chromosome movements/interactions define the phases of the overall continuous process. The correspondence between the phases of meiosis and the events of importance is as follows: *prophase I*-homologous pairing and recombination or crossing over,[6] *metaphase I*-alignment of homologous pairs of chromosomes (alignment I), *anaphase I*-segregation of homologues to separate nuclei (segregation I) [transition from meiosis I to meiosis II], *metaphase II*-alignment of individual 'replicated'[7] chromosomes (alignment II), and *anaphase II*-segregation of sister chromatids to separate nuclei (segregation II). Although the phase names (prophase, metaphase, etc.) have historical and cytological importance, they are not particularly descriptive of the subprocesses they represent. For this reason, in the remainder of this paper, I use the more descriptive labels for the events that appear in parentheses rather than the conventional phase names. While acknowledging that replication is not a part of the process of meiosis, I will subsequently group it with the six meiotic events because it is a necessary prerequisite of meiosis.[8] Of the seven total events, six of them--replication, homologous pairing, alignment I, segregation I, alignment II, segregation II--necessarily occur when a cell nucleus undergoes meiosis. The seventh, crossing over, is not necessary for the completion of meiosis and its occurrence or lack thereof has a significant effect on the outcome of a single meiosis.

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[6] For the purposes of this presentation, I will continue to use only the term 'crossing over' to refer to this meiotic event.

[7] The term 'replicated' is used here to refer to entities having the structure of replicated chromosomes. At this point in meiosis, however, sister chromatids of these entities may or may not be identical to one another depending on the previous occurrence of crossing over and the specific genetic constitution of the cell/organism in question.

[8] A not uncommon meiosis misconception to be discussed is that DNA replication is actually part of the meiotic process.

Of particular importance are the relative positions of the centromere, gene(s) and crossover event(s).

Correct Features Common to All Participants' Meiosis Models

While the meiosis models exposed by the 10 participants displaying some flawed meiosis knowledge differed from one another and from the correct model, the models exposed by all 15 participants shared a set of correct features. First, in all proposed models, chromosomes (not necessarily correctly conceived) were the participating entities. Second, in all proposed models, the structure and/or spatial arrangements of the chromosomes changed through the successive occurrence of events that included DNA replication (chromosome duplication), pairing, crossing over, and two alignment/segregations[9] (though not necessarily in the correct order). Third, each alignment/segregation was associated with a cell division such that all proposed models, with two exceptions,[10] had the chromosomes present in an initial cell distributed first to two intermediate cells followed by the distribution of chromosomes in each of the intermediate cells into two final cells.[11]

Meiosis Misconceptions

As was noted earlier, the participants who displayed flawed meiosis models fell into two groups, those having only process misconceptions and those having both chromosome and process misconceptions. Chromosome misconceptions were

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[9] Alignment and segregation are grouped here because of the deterministic effect of each alignment on its subsequent segregation.

[10] All 15 participants exposed meiosis models that included the one-cell-to-two-cell-to-four-cell division pattern. However, two of them (one expert and one inexperienced novice) violated this pattern or constraints imposed by this pattern under certain circumstances related to specific meiotic event misconceptions.

[11] Although meiosis is one type of nuclear division, I refer to cell division for simplicity and because all participants included cytokinesis in their meiosis models. The apparent lack of distinction between nuclear and cell division may indicate a misconception about these processes that was not addressed in this study.

almost exclusively confined to the inexperienced novices while individuals at all levels of expertise exposed various process misconceptions. These included both event-specific and whole-process process misconceptions. I will further define and elaborate on each of the categories of misconceptions (i.e., chromosome misconceptions, and event-specific and whole-process process misconceptions) in the following subsections.

Chromosome Misconceptions

One experienced novice and all five inexperienced novices harbored chromosome misconceptions. I will subsequently refer to these participants as the *alternate chromosome model* participants. While all of the alternate chromosome model participants knew that chromosomes consist of DNA and that this DNA contains linear arrays of genes, they exposed two general categories of chromosome misconceptions: (1) misconceptions about the structures of unreplicated and replicated chromosomes and (2) misconceptions about the origin of entities consisting of two chromatids and a centromere. The second category contains two subcategories: (2a) misconceptions in which entities having the two-chromatid-plus-centromere structure originates, not as a result of replication, but rather as a result of certain (incorrect) chromosome manipulations that occur during meiosis and (2b) misconceptions in which chromosome structure is somehow a function of chromosome number or ploidy. Individual alternate chromosome models contained anywhere from one to all three (i.e., (1), (2a), and (2b)) types of misconceptions.

Type-(1) chromosome misconceptions. Four of the 6 alternate chromosome model participants employed a chromosome model wherein the two subunits (sister chromatids) of replicated chromosomes were not physically attached to one another at any time during the process of meiosis. While the three inexperienced novices

among these four participants acknowledged the centromere attachment of the two subunits as a direct result of replication, the experienced novice in this group apparently did not consider centromeres or physical attachment of sister chromatids to be characteristics of replicated chromosomes. These four participants all had correct knowledge concerning unreplicated chromosome structure. In a fourth inexperienced novice's model of replicated chromosome structure, each chromatid consisted of a pair of identical double-stranded DNA molecules so that the whole entity contained not two, but four double-stranded DNA molecules. The two pairs of DNA molecules were attached by a centromere. Unreplicated precursors of these chromosomes contained two double-stranded DNA molecules connected by a centromere.

Type-(2a) chromosome misconceptions. The experienced novice and one inexperienced novice in the alternate chromosome model group harbored chromosome misconceptions of type (2a). In the experienced novice's meiosis model, single, rather than paired, replicated chromosomes aligned and separated during meiosis I and homologous chromatids then joined in the resulting intermediate cells to form two-chromatid-plus-centromere entities. In the inexperienced novice's meiosis model, two-chromatid-plus-centromere entities were formed as a result of her ill-conceived four-chromatid-plus-centromere replicated chromosomes separating into two two-chromatid entities at the first meiotic division.

Type-(2b) chromosome misconceptions. While type-(2a) misconceptions were not that common, chromosome misconceptions of type-(2b) are apparently quite prevalent among introductory biology/genetics students. Three (possibly 4)[12] of the 5 inexperienced novices in my study exposed this misconception and many other

[12] Because of some ambiguity in my data, I could not establish with certainty the presence of this type of misconception though it seems quite likely.

authors have reported the existence of, at least one form of, this misconception among both high school and college students (Brown, 1990; Fisher et al., 1986; Moll & Allen, 1983; Smith, 1990; Stewart, & Dale, 1989; Stewart, Hafner, & Dale, 1990). I have recently provided a detailed treatment of type-(2b) misconceptions (Kindfield, in press), so will only present a brief overview here.

Type-(2b) misconceptions are characterized by the association of chromosome structure with ploidy. In its most general form, the ploidy/structure misconception can be thought of as follows:

- chromosomes consisting of a single double-stranded DNA molecule (entities that one would correctly consider *unreplicated* chromosomes) are the kind of chromosomes that are present in haploid nuclei and
- chromosomes consisting of two double-stranded DNA molecules or chromatids (entities that one would correctly consider *replicated* chromosomes) are the kind of chromosomes that are present in diploid nuclei.

The most common form of type-(2b) misconceptions, harbored by 3 or 4 of my inexperienced novices and reported by others (see above), is as follows (illustrated in Figure 4): The two-DNA-molecule chromosomes that are present in diploid nuclei are formed, not by the process of replication, but rather when two single-DNA-molecule chromosomes, one from each parent, join each other at the centromere region when two haploid gametes fuse to produce a diploid zygote. Two of the 3 inexperienced novices who exposed this form of type-(2b) misconceptions also revealed additional misconceptions of this type. In one of these participant's meiosis model, two-chromatid-plus-centromere entities also arose as a result of replication occurring in the haploid product nuclei of meiosis which simultaneously changed these nuclei from haploid to diploid. The other inexperienced novice, who also believed that replicated chromosomes consisted of four chromatids, identified nuclei containing single-DNA-molecule entities as haploid (N), those containing two-DNA-molecule entities as diploid (2N), and those

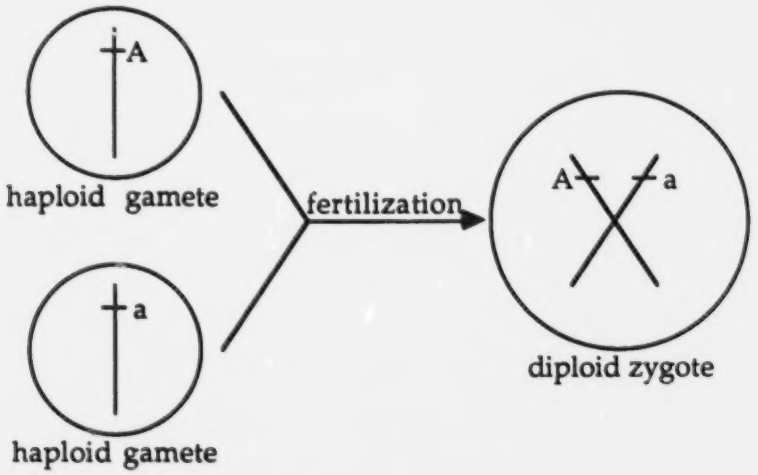


Figure 4. Formation-by-fertilization chromosome misconception. Each haploid gamete contains single-DNA-molecule chromosomes, represented here by lines labeled with the A and a alleles respectively. The diploid zygote contains a two-DNA-molecule chromosome formed by the joining of the A and a single-DNA-molecule chromosomes upon fertilization.

containing four-DNA-molecule entities as tetraploid (4N). Thus, she proposed a direct correspondence between the number of DNA molecules comprising an individual chromosome and the ploidy of nuclei in which chromosomes of that type occurred.

Event-specific Process Misconceptions

Three experts, 2 experienced novices, and all 5 inexperienced novices harbored event-specific process misconceptions. I will subsequently refer to these participants as the *alternate process model* participants. As was noted earlier, each of the meiosis models exposed by the alternate process model participants was unique. Further, several of these participants actually put forth more than one unique model for the process. In order to first provide a sense of what each of these models was like, they are presented schematically in Figure 5. (For more detailed descriptions of each individual model, see Hildebrand, 1989.)

While the alternate process models displayed by each of the alternate process model participants were different, subsets of individual models contained similar misconceptions about particular meiotic events. In general, the events around which participants exposed misconceptions are replication, crossing over, and alignment/segregation.[13] In Figure 6, participants' misconceptions are categorized according to the relative timing and structure/spatial arrangement aspects of each of these events. Misconceptions about the timing and nature of the remaining meiotic event, chromosome pairing, occurred in relation to misconceptions about the three events covered in Figure 6 and is therefore addressed in the context of these three events.

[13] Meiosis I and II have not been indicated for alignment/segregation because, with one exception, alignment/segregation misconceptions included both occurrences of alignment/segregation.

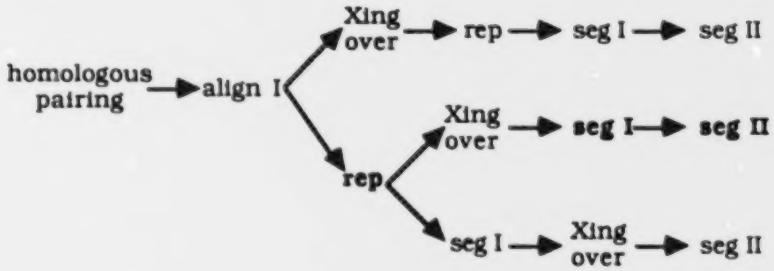
Figure 5. Correct and alternate process model participants' meiosis models. In each model presented, the temporal order of meiotic events is indicated by their horizontal order with the left-most event being the first in a given model. Comparison of alternate models with the correct model reveals incorrect knowledge about the relative order of events. Boldface type indicates that structure and process knowledge for a particular event was essentially correct in a given model and plain type indicates incorrect structure and/or process knowledge for that event. Events appearing in square brackets were not offered by the participant but would be necessary for completion of meiosis as described by the participant. Event names have been abbreviated as follows: rep=replication, Xing over=crossing over, align=alignment, and seg=segregation with Is and IIs indicating the stage of meiosis. In each model title, level of expertise of the participant is indicated by E=expert, EN=experienced novice or IN=inexperienced novice, different participants within expertise level are indicated by number, and titles marked with * indicate those participants who also had alternate chromosome models.

(Figure 5 continued on next page)

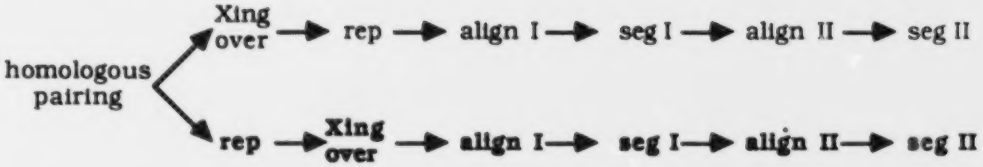
Correct Model of Meiosis

E3 Alternate Model

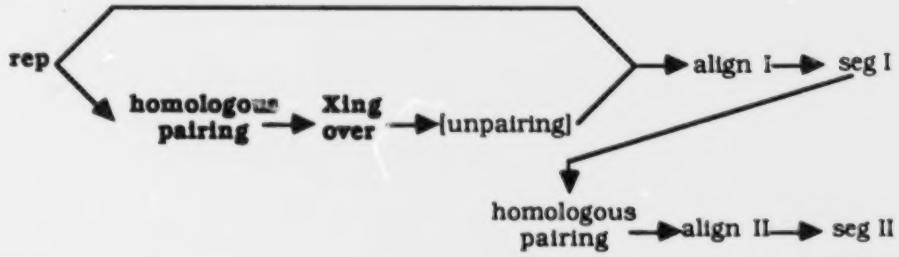
E4 Alternate Model



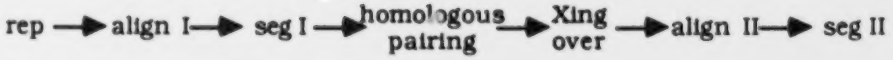
E5 Alternate Model



EN4 Alternate Model



EN5 Alternate Model*



(Figure 5 continued on next page)

IN1 Alternate Model*

<u>no Xing over</u>

homologous pairing → align I → seg I → rep → seg II → rep

<u>with Xing over</u>

nonhomolgous pairing → Xing over → [unpairing] → [random pairing] → align I → seg I

rep → "homologous" pairing → Xing over → seg II → rep

These four events occur in only ONE intermediate cell and this single cell produces FOUR final cells.

IN2 Alternate Model*

<u>Model 1</u>

rep → align I → seg I → homologous pairing → align II → seg II

<u>Model 2</u>

seg I → rep → seg II

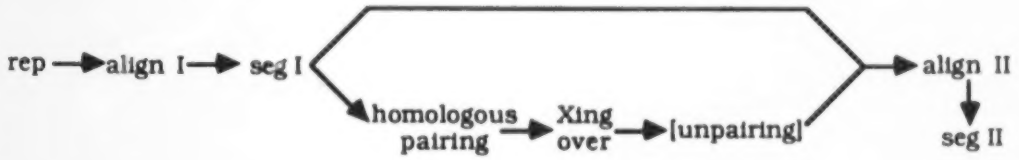
<u>Xing over</u>

rep → **homologous pairing** → Xing over → seg

IN3 Alternate Model*

rep → align I → seg I → homologous pairing → align II → seg II

IN4 Alternate Model*



IN5 Alternate Model*

rep → align I → seg I → Xing over → seg II

Replication (Participants E3 and EN4 exposed no incorrect replication knowledge.)

Timing misconceptions

1) occurs during meiosis I, specifically in relation to Xing over-E4, E5

2) occurs during meiosis I, not in relation to Xing over-IN4, IN5

3) occurs during and after meiosis II-IN1

4) contradiction in exposed model-before segregation I/Xing over & during meiosis II-IN2

Structure misconceptions

1) sister chromatids not connected as a result of replication-EN5

2) sister chromatids not connected at any time during meiosis-IN1, IN2 (?), IN3

3) four chromatids per replicated chromosome-IN5

4) replicated chromosome structure not explicated-IN4

Crossing over (Participant EN4 exposed no incorrect Xing over knowledge.)

Timing misconceptions

1) can occur during meiosis I either before or after (correct) replication-E4, E5

2) can occur during meiosis II between chromosomes in different intermediate cells (stage violation)-E4

3) can occur during meiosis I and/or meiosis II-IN1

4) occurs during meiosis II between chromosomes in the same intermediate cell-EN5, IN4, IN6

Structure misconceptions

1) incorrect participating structures

(a) occurs between unreplicated homologues-E4 & E5 (pre-replication Xing over)

(b) occurs between replicated homologues separated by segregation I-E4 (post-segregation I Xing over)

(c) occurs between unreplicated nonhomologues-IN1 (meiosis I Xing over)

(d) occurs between various incorrect structures in intermediate cells -EN5, IN1 (meiosis II Xing over/stage violation), IN4, IN5

2) relative positions of the centromere, gene(s), and crossover events(s) irrelevant

(a) in the context of correct timing and chromosome structure knowledge -E3, E4 (post-replication Xing over), IN2

(b) in the context of incorrect timing and chromosome structure knowledge-IN1

(c) in the context of incorrect timing and/or chromosome structure knowledge wherein the relative positions are truly irrelevant-EN5, IN4, IN5

(Figure 6 continued on next page)

Alignment/Segregation (Participants E3 and E5 exposed no incorrect align/seg knowledge.)

Timing misconceptions

1) alignment I follows homologous pairing and precedes replication/Xing over-E4

2) alignment I not preceded by correct events but correctly followed by segregation I
-EN4, EN5, IN1, IN2, IN3, IN4, IN5

3) alignment II not preceded by correct events but correctly followed by segregation II
-EN4, EN5, IN2, IN3, IN4

4) alignment II not mentioned and segregation II not preceded by correct events-IN1, IN5

Structure misconceptions

1) alignment I-paired, unreplicated chromosomes align and remain so until segregation I proceeds normally-E4

2) alignment I/segregation I-individual replicated chromosomes line up and sister chromatids pull apart

alignment II/segregation II-homologous chromatids (unreplicated chromosomes) pair, line up, and pull apart

-EN5 (homologous chromatids also become connected by a centromere), EN4, IN2 (Model 1), IN3

3) alignment I/segregation I -in the absence of Xing over, unreplicated homologues pair, line up, and pull apart
-in the event of meiosis I Xing over, unreplicated post-Xover chromosomes randomly pair, line up, and pull apart

alignment II/segregation II-alignment II output/segregation II input structures not explicated

-IN1

4) alignment I/segregation I-individual "diploid" chromosomes line up and subunits pull apart

alignment II/segregation II-individual chromatids line up and one of each homologue pulled to each pole

-IN4

5) alignment I/segregation I-individual, replicated "diploid" chromosomes line up and two-DNA-molecule subunits pull apart

alignment II/segregation II-alignment II output/segregation II input structures not explicated

-IN5

Figure 6. Categories of event-specific process misconceptions exposed by the alternate process model participants. Participants are identified by level of expertise and number. Xing over=crossing over. Input and output structures refer to chromosome configurations that precede and follow each event.

There are several notable patterns among the specific process misconceptions exposed about the three problematic events. Brief descriptions of these patterns are provided in the three subsections that follow. The purpose of these sections is to highlight misconceptions common to more than one participant. Thus, not all misconceptions listed in Figure 6 are addressed here. Participants are identified by codes in these subsections for easy reference to Figures 5 and 6 (where E=expert, EN=experienced novice, and IN=inexperienced novice and numbers refer to different individuals).

Replication misconceptions. As was described earlier, only a subset of the alternate chromosome model participants had misconceptions about the structure of replicated chromosomes. Two correct chromosome model experts (E4 & E5) as well as four alternate chromosome model inexperienced novices (IN1, IN2, IN4, & IN5) had misconceptions about the timing of replication. The experts' misconception specifically involved ambiguity about the relative timing of replication and crossing over during meiosis I. In contrast, inexperienced novices proposed that replication occurred at a variety of incorrect times during meiosis, none of which were related to crossing over. While the experts' misconception about the timing of replication has a particular focus that distinguishes it from that of the inexperienced novices, a common higher-level feature is worth noting: Namely, none of these participants were aware of the temporal separation of the process of replication and the process of meiosis in the eukaryotic cell cycle (see footnote 4 for explanation).

Crossing over misconceptions. Experts E4 and E5 crossing over misconceptions primarily involved the relative timing of replication and crossing over. While both displayed the correct knowledge that crossing over occurs between paired, replicated chromosomes, they shared the misconception that crossing over could also occur prior to replication between paired, unreplicated chromosomes. This misconception necessarily includes the related misconception that pairing can occur

before replication. One of these experts (E4) exhibited the additional timing and related structure misconceptions that crossing over could also occur between nonsister chromatids of replicated chromosomes (correct) that had already been physically separated by segregation I (a unique violation of stage knowledge). The fact that each of these experts proposed at least two different temporal positions for crossing over indicates that neither recognized that each meiotic event occurs only once at a unique position in the sequence of events that constitute the process of meiosis.

In addition to the preceding misconceptions, expert E4 also shared a third expert's (E3) only process misconception wherein neither recognized the significance of the presence and position of the centromere to crossing over (significant to E4's model when crossing over occurs between replicated chromosomes). While E3 disregarded the presence of the centromere altogether, E4 did recognize the significance of the centromere position when crossing over occurs between a gene and the centromere but denied the significance of the centromere position when crossing over occurs between two genes on the same chromosome (which also necessarily includes a crossover between one of those genes and the centromere).

In three of the six models of crossing over proposed by the alternate chromosome model participants (EN5, IN4, and IN5), the presence and position of the centromere is irrelevant to the outcome of meioses in which crossing over occurs. The feature common to these three models that renders the centromere insignificant is that they include the timing misconception that crossing over occurs during meiosis II. Misconceptions about participating structures necessarily follow from this timing misconception with each participant in this subgroup proposing different incorrect participating structures depending on their individual alternate chromosome models and additional alignment/segregation misconceptions.

Of the two remaining models of crossing over put forth by the alternate chromosome model participants, that proposed by inexperienced novice IN2 includes the correct timing for crossing over. However, IN2, like experts E3 and E4, did not recognize the significance of the presence or position of the centromere to crossing over. IN2 differed from the two experts, however, in that both experts ultimately recognized the significance upon prompting and IN2 did not. Most features of the final ill-conceived model for crossing over (that of IN1) were unique and therefore are not addressed here.

While all participants who had models for crossing over shared the correct knowledge that crossing over occurs between paired chromosomes, three of them (EN4, IN1, & IN4) conceived of pairing as a component of crossing over rather than as an independent meiotic event that must precede crossing over. All three of these participants proposed meiosis models in which chromosomes paired for crossing over would had to have unpaired immediately following crossing over in order to complete meiosis according to their respective models.

Alignment/Segregation misconceptions. Of the expert alternate process model participants, only expert E4 displayed a misconception falling into the alignment/segregation category. Her misconception was confined to alignment I and had no adverse effect on the normal occurrence of segregation I and the rest of meiosis. In contrast, the alignment/segregation misconceptions exposed by the remaining alternate process model participants encompassed both occurrences of alignment/segregation and diverged significantly from the correct model of meiosis. This group includes correct chromosome model participant EN4 and all six alternate chromosome model participants.

The seven participants in the latter group all recognized that segregation I and II result in the formation of the intermediate and final meiotic products respectively, and most of them accurately proposed that an alignment event preceded each

segregation event. Thus the timing of these events with respect to knowledge of the two stages of meiosis was correct. However, timing misconceptions about which events preceded alignment I often in conjunction with participants' alternate chromosome models resulted in a variety of alignment/segregation structure misconceptions among these participants.

Participants EN4, EN5, and IN3 shared the same alignment/segregation misconception wherein the characteristics of alignment I and alignment II were basically switched, meaning that single (rather than paired) replicated chromosomes align in the initial nucleus during meiosis I and homologous chromosomes pair and align in each intermediate nucleus during meiosis II. The homologues in each intermediate nucleus are the chromatids or unreplicated chromosomes that separated as a result of segregation I. These unreplicated homologues then separate via segregation II to give rise to the four final meiotic products. This misconception was also implied in participant IN2's Model 1 for meiosis. An inherent component of this alignment/segregation misconception is the misconception that pairing occurs during meiosis II rather than during meiosis I.

Figure 7 illustrates alignment I and II for this misconception. This figure accurately represents participant EN4's model of meiosis applied to gamete set (i) (see Figure 1) including his spontaneously-generated diagrams. Sister chromatids of replicated chromosomes would not be connected in participant EN5 and IN3's (and possibly participant IN2's) alignment I configuration diagrams because of their respective replicated chromosome structure misconceptions. In addition, homologous chromatids would, in their most complete representation, be connected by centromeres in participant EN5's alignment II configuration diagrams because of her misconception about the origin of two-chromatid-plus-centromere entities.

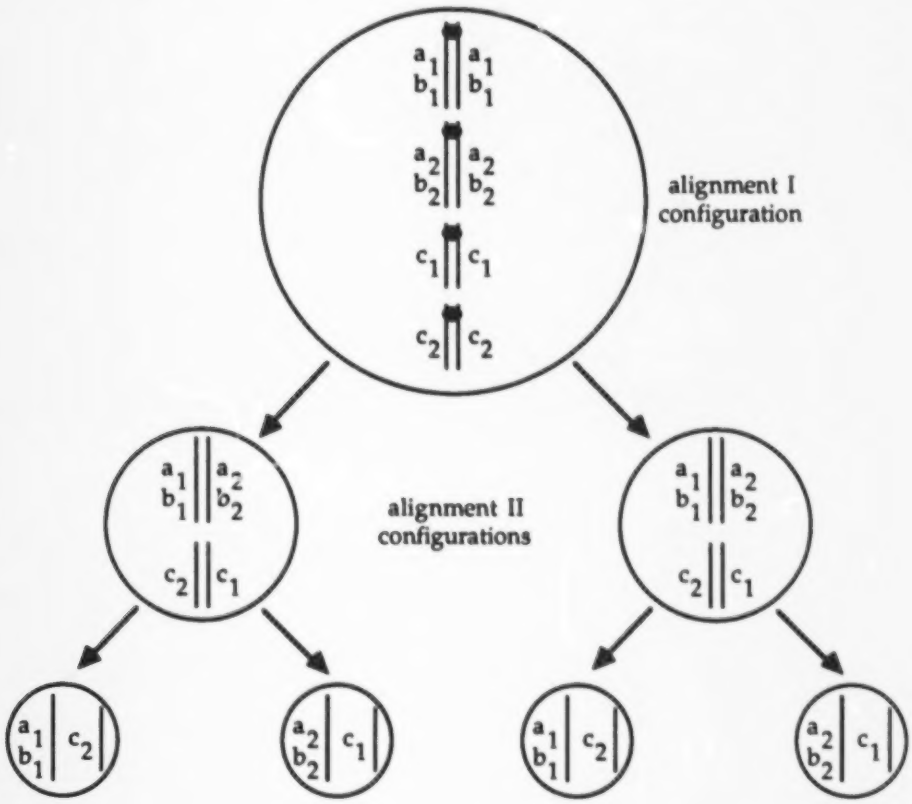


Figure 7. Canonical pictorial representation of the alignment/segregation misconception exposed by participants EN4, EN5, IN2 (Model 1), and IN3. Replicated chromosomes in the alignment I configuration consist of two sister chromatids (each represented by a single line) attached at the centromere (represented by a dot). Chromosomes in the alignment II configurations consist of paired, unreplicated homologues (each represented by a single line).

Participants IN4 and IN5 exhibited a similar alignment I misconception wherein single rather than paired entities line up in the center of the initial cell. Participant IN4 called these single entities "diploid" chromosomes, consisting of two chromatids, one from each parent, and a centromere. In participant IN5's models, each single entity was a replicated chromosome containing four attached chromatids, two from each parent. In IN4's model, the two chromatids of each "diploid" chromosome pulled apart from one another during segregation I. In IN5's model, pairs of chromatids from each replicated chromosome separated as a result of segregation I. The remainder of their alignment/segregation misconceptions were unique and therefore are not addressed here.

Whole-process Process Misconceptions

In addition to misconceptions about specific meiotic events, all but two of the alternate process model participants exhibited anywhere from one to three whole-process process misconceptions. These misconceptions involve knowledge about the process of meiosis as a whole as opposed or in addition to knowledge about individual components of the process.

In the first whole-process misconception, participants E4, E5, IN1, IN2, IN4, and IN5, put forth alternate models wherein the process of replication was considered to be part of the process of meiosis rather than the two processes being temporally separated from one another. This misconception is both event specific and whole process: event specific in the sense that it concerns the relative timing of a cellular event necessary for meiosis and whole process in the sense that it involves the relationship between two distinct cellular processes (i.e., replication and meiosis).

The second whole-process misconception, also related to event timing, was that certain events could occur at more than one temporal position in the sequence of events that constitute meiosis rather than each event occurring once at a unique

time. Participants E4 and E5 exhibited this misconception in relation to crossing over, participant IN1 in relation to crossing over and replication, and participant EN4 in relation to homologous pairing when crossing over occurs.

The third whole-process misconception involves the event-specific misconception harbored by participants EN4, IN1, and IN4 that pairing is a component of crossing over. The whole-process aspect of this misconception is the lack of recognition that each chromosomal activity that occurs during meiosis is an activity that, while requiring specific preceding activities, occurs independently of other activities. For example, in the correct model of meiosis, crossing over requires that homologous chromosomes be paired, but homologous pairing occurs at the beginning of meiosis regardless of the subsequent of occurrence of crossing over.[14]

An interesting feature of these whole-process misconceptions is that their correction would have the effect of eliminating specific event misconceptions, in some cases transforming an alternate meiosis model into one that is completely consistent with the correct model. If participants E4 and E5 had recognized that each event occurs at one unique time, their models would have lost their incorrect multiple-path character, bringing them one step closer to being correct models of meiosis. E5's model would have been completely correct and E4's model would have been nearly correct in the context of correct knowledge about the temporal separation of replication and meiosis. Given participant EN4's correct knowledge about the timing of crossing over, his recognition that pairing and crossing over are independent events and that pairing occurs only once during meiosis could have stimulated the correction of his alignment/segregation misconception and thus of his overall model of meiosis. Because participant IN1, IN2, IN4, and IN5's meiosis

[14] The meiosis models put forth by participant IN2 are distinct alternatives rather than being pieces of a single overall model. For this reason, they were considered separately when being assessed for the presence of whole-process misconceptions. While the first whole-process misconception was a component of each of her alternate models, no individual alternate as described by IN2 contained either of the remaining whole-process misconceptions.

models deviated more severely from the correct model than those of E4, E5, and EN4, recognition of whole-process misconceptions among inexperienced novices would not have corrected their models. However, correct knowledge about applicable whole-process concepts could have decreased the extent to which each alternate model deviated from the correct model.

Summary of Meiosis Misconceptions

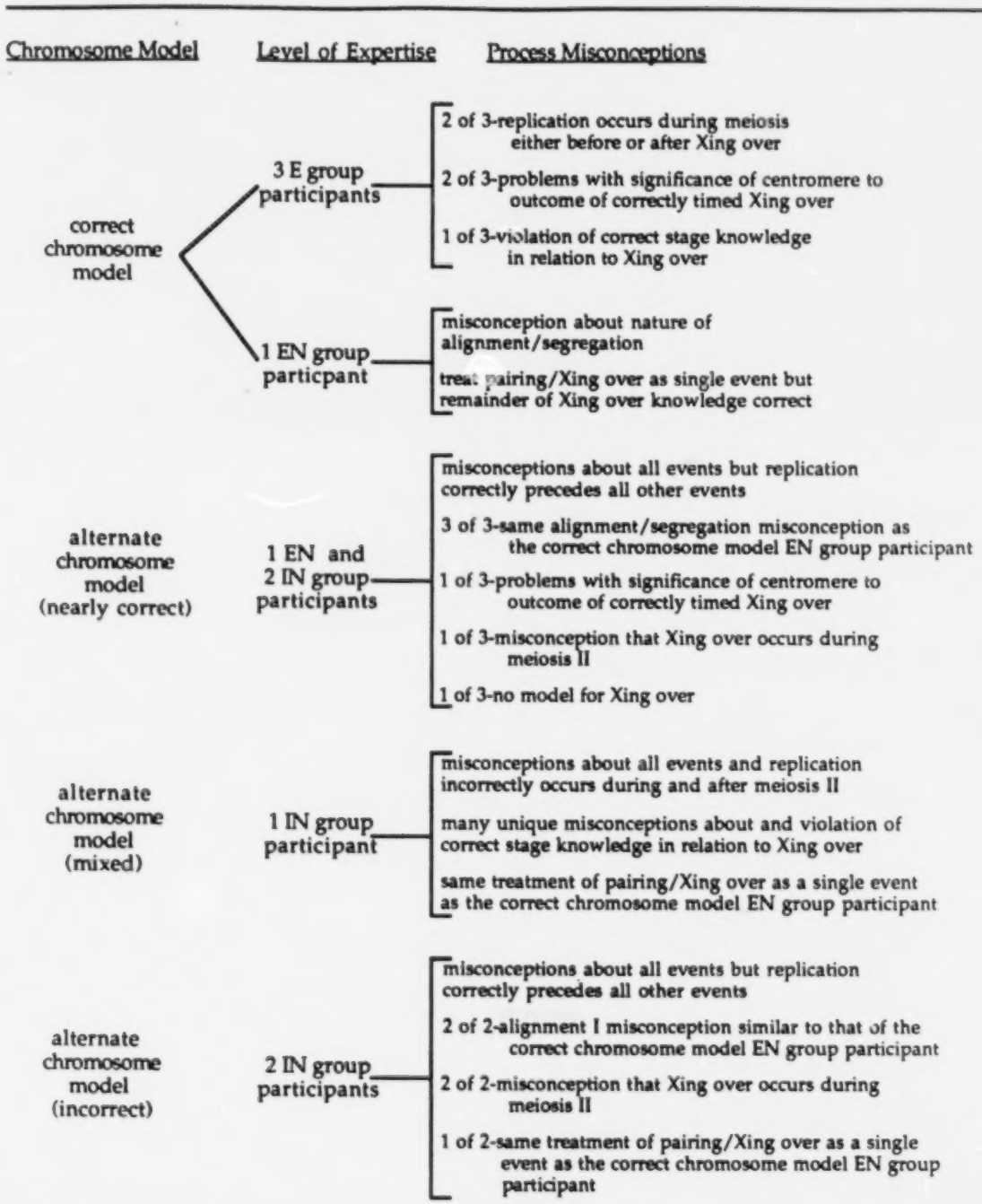
The chromosome and process misconceptions discussed in the preceding sections are summarized in Figure 8. This figure is useful not only as a summary, but also as a means for extracting broader relationships from the compiled intricacies of individuals' specific meiosis models. Two notable relationships are that between chromosome and process knowledge and that between misconceptions and level of expertise.

Relationship between chromosome and process knowledge. The existence of the correct chromosome model alternate process model class of participants demonstrates that having a correct chromosome model does not insure having a correct process model. Further, given the types of process misconceptions exhibited by participants in this class, it appears that having a correct chromosome model does not restrict process misconceptions to particular meiotic events. This point is additionally supported by the fact that the nearly correct alternate chromosome model participants, who conceived of meiosis as starting with close to correctly structured entities, harbored misconceptions about all meiotic events.

While having a correct or nearly correct chromosome model does not preclude having process misconceptions, a correct chromosome model is a necessary component of a completely correct process model however. Theoretically, unless meiosis is conceived of as starting with entities of correct structure and origin, even properly timed meiotic events will occur with incorrectly structured entities. This

Figure 8. Summary of chromosome and process models put forth by the 10 alternate process model participants. Participants having correct chromosome models are separated into two groups according to the types of event misconceptions present in their alternate process models. Participants having alternate chromosome models are separated into three groups according to the degree to which their alternate chromosome models deviated from the correct chromosome model. A nearly correct alternate chromosome model is one in which the identical subunits of a replicated chromosome are not connected to one another at any time during meiosis. A mixed alternate chromosome model is one in which two-chromatid-plus-centromere entities have two origins: replication (correct) and the joining of pairs of unreplicated, homologous chromosomes upon fertilization (incorrect). An incorrect chromosome model is one in which two-chromatid-plus-centromere entities originate from the joining of pairs of unreplicated, homologous chromosomes upon fertilization. The level of expertise of subjects falling into each group is indicated by the standard letter designations: E = experts, EN = experienced novices, and IN = inexperienced novices.

(Figure 8 continued on next page)


Chromosome Model
Level of Expertise
Process Misconceptions
correct chromosome model
3 E group participants
2 of 3-replication occurs during meiosis either before or after Xing over
2 of 3-problems with significance of centromere to outcome of correctly timed Xing over
1 of 3-violation of correct stage knowledge in relation to Xing over
1 EN group particpant
misconception about nature of alignment/segregation
treat pairing/Xing over as single event but remainder of Xing over knowledge correct
alternate chromosome model (nearly correct)
1 EN and 2 IN group participants
misconceptions about all events but replication correctly precedes all other events
3 of 3-same alignment/segregation misconception as the correct chromosome model EN group participant
1 of 3-problems with significance of centromere to outcome of correctly timed Xing over
1 of 3-misconception that Xing over occurs during meiosis II
1 of 3-no model for Xing over
alternate chromosome model (mixed)
1 IN group participant
misconceptions about all events and replication incorrectly occurs during and after meiosis II
many unique misconceptions about and violation of correct stage knowledge in relation to Xing over
same treatment of pairing/Xing over as a single event as the correct chromosome model EN group participant
alternate chromosome model (incorrect)
2 IN group participants
misconceptions about all events but replication correctly precedes all other events
2 of 2-alignment I misconception similar to that of the correct chromosome model EN group participant
2 of 2-misconception that Xing over occurs during meiosis II
1 of 2-same treatment of pairing/Xing over as a single event as the correct chromosome model EN group participant

assessment is supported by the facts that (1) the five participants who had correct process models also had correct chromosome models and (2) the mixed and incorrect alternate chromosome model participants, who conceived of meiosis as starting with incorrectly structured chromosomes, have process misconceptions concerning all meiotic events all of which included misconceptions about event-specific chromosome structure.

Relationship between misconceptions and level of expertise. In general, expert participants' alternate models contained the fewest flaws with misconceptions primarily confined to various aspects of the one variable meiotic event, crossing over, and no chromosome misconceptions. Both groups of novice participants' alternate models included flaws about one or more of the necessary events (replication, pairing, alignment I, segregation I, alignment II, and segregation II) as well as crossing over. Chromosome misconceptions were rare among the experienced novices and common to all inexperienced novices, and process misconceptions about all events occurred among those novices who also had chromosome misconceptions. Certain individual event misconceptions were shared by participants at all three levels of expertise, but overall, the inexperienced novice participants displayed the most deviant meiosis models. In addition, while their chromosome models deviated to varying degrees from a correct chromosome model, inexperienced novices were the only participants to exhibit a unique misconception about the origin of two-chromatid-plus-centromere entities and inappropriately related the concept of ploidy to chromosome structure.

Quality of Participants' Overall Models of Meiosis

Another set of qualities or characteristics, in addition to particular misconceptions, distinguish the alternate models displayed by the inexperienced novices from the meiosis models put forth by the experts and experienced novices.

These characteristics are completeness, stability, and internal consistency. Both the correct and alternate meiosis models utilized by the more experienced participants were complete in the sense that they generally accounted for replication and the six meiotic events.[15] The models exhibited by these participants were considered to be stable because each of these participants consistently applied the same meiosis model across all three gamete sets.[16] Finally, the more experienced participants' models were internally consistent in that even alternate process models exposed by these participants could successfully account for the distribution of chromosomes from the initial diploid nucleus into the four final haploid nuclei.

In contrast to the expert and experienced novice participants, the alternate meiosis models put forth by the inexperienced novice participants tended to be incomplete, unstable, and/or internally inconsistent. While differing in terms of specific contributing factors, four of the five inexperienced novices (IN1, IN2, IN3, IN4) displayed incomplete models, three of the five (IN1, IN2, IN5) exhibited model instability, and two of the five (IN1, IN5) proposed models that were internally inconsistent.

Discussion

The results presented here are suggestive of both sources of the numerous misconceptions displayed by the research participants and a model of how individuals might construct a sound understanding of meiosis. Both have implications for meiosis instruction. In the following sections, I address both in conjunction with their respective educational implications. (For details concerning

[15] While several of the more experienced participants did not refer to alignment I and/or alignment II, their correct knowledge about segregation I and II implied correct knowledge about the respective alignment events. In these cases, lack of expression of alignment knowledge was not viewed as denoting the existence of an incomplete model.

[16] Although expert E4 and E5's models contained multiple temporal positions for crossing over, their models were not considered unstable because they proposed multiple occurrences of crossing over as part of their respective models as opposed to proposing contradictory models.

an integrated form of instruction that addresses all exposed misconceptions and the knowledge construction model to be discussed, see the section on Diagram-oriented-cell-cycle-based Instruction in Hildebrand, 1989.)

Sources of Meiosis Misconceptions and Related Educational Implications

Chromosome Misconceptions

Of all chromosome misconceptions, two were rather common: the beliefs that sister chromatids are not attached to one another at any time during meiosis and that chromosome structure is a function of ploidy. The former may be related to the misconception that single entities align and their subunits segregate during meiosis I (see Alignment/Segregation Misconceptions below), in that the subunit attachment is viewed as quite transient in light of the imminent separation. Reinforcing the fact and importance of (i.e., proper segregation of genetic information) sister chromatid attachment in instructional settings may have the added benefit of assisting in building a correct model of alignment I.

With regard to the ploidy/structure misconception, my own detailed analysis of this misconception, possible sources, and instructional implications appears in Kindfield (in press) Thus, I provide a briefer version here. The following factors appear to contribute specifically to the form of the misconception in which two-chromatid-plus-centromere entities are formed when (unreplicated) homologous chromosomes from haploid cells join in the nucleus of a newly formed diploid nucleus of a zygote:

- the inherent satisfaction of having chromosomes from each parent physically join upon fertilization (the "romantic" view),
- the fact that haploid cells are typically depicted as containing *unreplicated* chromosomes,
- the fact that diploid cells are typically depicted as containing *replicated* chromosomes, and

- the fact that the nature of chromosome duplication and the origin of two-DNA-molecule chromosomes is often not clarified in instruction.

In addition, standard explanations of how ploidy changes as a cell cycle proceeds may contribute to the incorrect connection between ploidy and structure. Not only do two different explanations exist, but one of them includes the notion that ploidy does in fact change as a result of replication. When interpreted properly, this explanation does not associate ploidy with chromosome structure. However, for the novice, standard explanations of ploidy can, at best, be confusing and, at worst, contribute to the formation of the ploidy/structure misconception.

The prevalence of the ploidy/structure misconception among introductory students, its likely instructional sources, and the necessity of having a correct chromosome model to having a correct process model plainly indicate a need for instruction that (1) clearly defines the origin of two-chromatid-plus-centromere entities and (2) clearly distinguishes between the concepts of chromosome structure and chromosome number. A general approach for dealing with both of these instructional goals is to present general changes in chromosome structure and ploidy as well as both nuclear division processes in the context of the eukaryotic cell cycle and representative eukaryotic life cycles. Because of the potential for confusion associated with the details of the standard descriptions of how ploidy changes during the cell cycle, I advocate avoiding these descriptions in introductory instruction. If included, great care must be taken in disassociating ploidy, as it is being defined in each description, from chromosome structure. All components of this instruction should include carefully constructed and clearly defined diagrams that serve as both illustrations and more importantly as tools for understanding and reasoning about the concepts at hand.

Event-specific Process Misconceptions

Replication Misconceptions The prevalence of the misconception that replication occurs during meiosis among inexperienced novices[17] and its occurrence among experts suggests that the relative timing of replication is a somewhat elusive piece of knowledge about meiosis and more generally about cell cycles. A likely source of this misconception is the separation of concepts of replication and cell division processes in standard genetics instruction which has been documented by several genetics-learning researchers (Balls & Godsell, 1973; Cho et al., 1985; Cochrane & Dockerty, 1984; Longden, 1982). The lack of explicit instruction about the temporal relationship between replication and cell division processes in conjunction with the general knowledge that replication must happen sometime before nuclear division is complete may result in the inappropriate placement of replication during meiosis.

While conceiving of replication as occurring during meiosis (or mitosis) prior to any other meiotic events has no effect on the potential correctness of the rest of a meiosis (mitosis) model, having replication occur during meiosis makes little biological sense when one considers the nature of the replication process and the nature of the DNA during meiosis. DNA molecules must be relatively dispersed and open for the process of replication to occur, whereas these same DNA molecules must be condensed and tightly coiled during the nuclear division processes of mitosis and meiosis. If, in addition to the development of understanding of meiosis, the goals of biology instruction include the development of understanding of constraints associated with various subcellular processes and how those processes relate to one another, then the replication timing misconception is a reflection that they are not achieved.

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[17] This misconception has also been reported in other studies of student misconceptions (Longden, 1982; Moll & Allen, 1983; Smith, 1990).

As was noted in conjunction with chromosome misconceptions, a likely mechanism for aiding the construction of a realistic view of the relationship between replication and meiosis is to teach about meiosis in the context of the eukaryotic cell cycle. Especially when accompanied by thoughtfully constructed diagrams, this approach can reinforce the temporal separation of replication and meiosis as well as clearly establish the roles played by each process in the cycle.

Crossing Over Misconceptions Many of the misconceptions and difficulties associated with crossing over are likely due to the complexity and subtlety of this meiotic event. With regard to subtlety, those experts who displayed misconceptions/difficulty about the significance of the relative positions of the centromere, gene(s), and crossover event(s) to the outcome of meiosis were individuals who did not deal with meiosis, particularly this aspect, on any regular basis. Even one expert who exposed a completely correct overall meiosis model, initially approached the relative position issue as if he needed to remind himself that it existed.

A common and less subtle crossing over misconception among the novices was the belief that crossing over occurs in each of the intermediate nuclei during meiosis II rather than in the initial nucleus during meiosis I. Interestingly, as a result of the gross timing misconception that places crossing over during meiosis II, the centromere no longer bears on the outcome of a meiosis in which crossing over occurs. The most likely source of this misconception is the novices' ad hoc application of their general knowledge that crossing over can occur at some time during meiosis while problem solving. In the meiosis problem's specification of the allelic constitution of the four final cells from each of three specific meioses, participants were given meiosis outcomes one stage removed from the precursor intermediate nuclei and two stages removed from the precursor initial nucleus.

Certain behaviors not reported in the results[18] indicated that participants who proposed meiosis II crossing over did so by first constructing intermediate cells that could give rise to a set of problem-specific final cells and then proposing crossover events in those cells to account for specific allelic combinations. In other words, these participants worked backward through meiosis, using the problem situation as a guide for deciding the timing of crossing over, rather than reasoning from a more completely formulated meiosis model in order to solve the problem.[19]

In a final crossing over misconception common to several novices pairing is a component of crossing over rather than an independent, necessary meiotic event that must precede crossing over. A likely source of the pairing/crossing over misconception is the lack of integration of crossing over into the overall meiosis models presented in instruction. Students most often learn first about meiosis as it occurs in the absence of crossing over, followed by instruction about crossing over. In this instruction, which focuses on crossing over rather than its relation to the rest of meiosis, the necessity of pairing is emphasized verbally and/or pictorially. If conditions are not provided for the integration of crossing over into the overall meiosis model, the initial separation of crossing over from meiosis may strengthen the association between pairing and crossing over and weaken the identification of pairing as an independent meiotic event.

All of these difficulties with crossing over can be dealt with in instructional settings through (1) clear illustration of the subprocess and its role in meiosis and

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[18] These behaviors were not considered in the results because the analysis was not an analysis of problem-solving strategies. They are mentioned here insofar as they bear on this particular misconception.

[19] This behavior differs substantially from certain expert behaviors in which individuals worked backward from a set of final cells in order to determine the specific nature of correctly timed crossing over. The novice behavior is similar to that reported by Stewart & Dale (1989) and Stewart, Hafner, & Dale (1990) in which high school students tended to generate meiosis models based on specific problem-solving outcomes (typically derived from the Punnett square algorithm). It is also analogous to the working backward strategy utilized by physics novices during problem solving (Larkin et al., 1980a, 1980b; Larkin & Reif, 1979).

(2) practice reasoning about individual instances of meiosis that include crossing over (like the meiosis problem used in this research). One might question the value of addressing the subtleties of crossing over in an introductory class. While perhaps not a topic on which a teacher can spend much time, it is certainly crucial to understanding how meiosis contributes to genetic variability (a necessary substrate for natural selection) and to understanding genetic linkage (the basis for the ever more popular search and discovery of markers for genetic diseases).

Alignment/Segregation Misconceptions. A feature common to most of the alignment/segregation misconceptions (exposed only by novices) was that unpaired entities align and equivalent subunits segregate during meiosis I.[20] In a majority of these cases, homologous entities then paired during meiosis II. Participants in this subgroup apparently knew that homologous chromosomes pair for one occurrence of alignment/segregation and not for the other, but they associated pairing with the wrong occurrence. A possible contributing factor to the misconception that single entities align during meiosis I is the comparison of meiosis to mitosis that is frequently made during meiosis instruction. Students are typically taught that alignment II during meiosis is like mitotic alignment in that individual, rather than paired, chromosomes align in the center of the nucleus. However, the intermediate nuclei in which alignment II occurs contain half the number of chromosomes as the initial nucleus in which alignment I or mitotic alignment would occur. Based on comments made during the interviews, students generally seemed to remember that one of the meiotic alignments is like a mitotic alignment where chromosomes do not pair. Given any uncertainty about the timing of pairing or of its occurrence as an independent event, students may opt for no pairing during alignment I because that alignment would be most like mitotic alignment, having the same

[20] This incorrect chromosome behavior was also proposed by college-level biology students interviewed by Moll & Allen (1983) and Smith (1990).

spatial arrangement and number of chromosomes. Again, clear illustration and practice reasoning about individual instances of meiosis along with side-by-side comparisons with mitosis may aid in ameliorating this misconception. Comparisons with mitosis should emphasize the fact that pairing is the first distinguishing feature between the two nuclear division processes and it occurs at the beginning of meiosis. Meiosis discussion and problem solving should go on to emphasize that once pairing occurs, chromosomes remain paired until another subprocess (segregation I) separates them.

Whole-process Process Misconceptions

Sources and implications of two whole-process process misconceptions, replication timing and pairing/crossing over as one event, have already been covered. The latter of these two and the third, individual meiotic events can occur more than once, might be ameliorated by the following change in typical instruction. In my meiosis review, I noted that standard phase names are not at all descriptive of the actual events that occur during each phase. So I chose to talk about events and to forego the use of phase names. In all of my interviews, the only time that a phase name was ever mentioned was in reference to the 'metaphase plate' by very few participants. Instead, participants also used terms more descriptive of actual events. Because of the descriptive, salient nature of these event names and a general view of process in which objects go through series of events or actions to produce products or outcomes, I advocate dropping phase names altogether from initial mitosis/meiosis instruction and using terms that instead explicitly denote chromosome movements/interactions. In so doing, I believe that the unique sequential occurrence of individual events can be made more experiential for students. Including an entire other set of cytologically important but somewhat esoteric terms at this stage of instruction only increases the amount of

stuff to be learned rather than clarifying any crucial issues. Once a reasonable meiosis model is established, phase names can be added if necessary.

Constructing Understanding and Related Educational Implications

Early on, I distinguished meiosis knowledge that was present and correct among all the participants in this study from knowledge about which the alternate model participants harbored a variety of misconceptions. This distinction as well the nature of particular misconceptions and model qualities observed among the participants serve as the basis for a model of how individuals construct an understanding of meiosis.[21] At this point in time, the model is somewhat speculative and is one focus of my current research. In the following subsections, I first present an overview of the model as currently conceived, elaborate on the overview, and discuss instructional implications of the model.

Overview of the Model of Constructing Understanding

Students are envisioned as entering meiosis instruction with generic process knowledge gleaned from previous experiences with common processes. This generic knowledge consists of knowledge about what generally constitutes a process, that is, that some object(s) undergo(es) a series of actions or changes that result in some outcome(s). Generic process knowledge serves as a framework for the accumulation and organization of basic or skeletal pieces of meiosis knowledge: namely, (1) chromosomes are the primary objects participating in this particular

[21] Because of the similarities between meiosis and mitosis, it is likely that previously constructed understanding of mitosis would somehow influence the construction of understanding of meiosis. The nature of this potential influence would be dependent on a variety of factors that were beyond the scope of the study reported here. For this reason, the potential influence is acknowledged but is not incorporated into the proposed model. Since the similarities between meiosis and mitosis are also likely to result in similar forms of knowledge construction, the proposed model is considered to be incomplete rather than flawed through the lack of inclusion of the role of previous exposure to mitosis.

process; (2) meiosis entails a series of chromosome movements/interactions including replication, pairing, crossing over, and two alignment/segregations; and (3) each alignment/segregation results in the production of two nuclei/cells from a single nucleus/cell. The result of this level of the construction of understanding is a core conception of meiosis. Continued construction of meiosis understanding involves the accumulation, organization, and reorganization of more detailed pieces of meiosis knowledge guided by the meiosis-specific core conception. Connections between specific pieces of knowledge in an individual's knowledge base constrain the meiosis model that the knowledge base can support. When all constraints are mutually compatible, the knowledge base will then support a correct overall model of meiosis. A key component of making the transition from the core conception of meiosis to an elaborated, correct model of meiosis is conflict resolution. Conflict resolution occurs when an individual is engaged in direct reasoning about meiosis and constraints inherent in his/her not completely correct model of meiosis are recognized as incompatible.

Elaboration of and Evidence for the Model of Constructing Understanding

In the model of constructing understanding, the basic or skeletal pieces of meiosis knowledge that contribute to the core conception correspond to those aspects of meiosis that were correctly conceived by all participants in this study. That these pieces of knowledge were correct in meiosis models of individuals at all levels of expertise suggests that skeletal knowledge components are relatively easily acquired even after limited instruction. The apparent ease of understanding these skeletal components along with their obvious correspondence to the components of a generic view of process underlie the proposal that students enter instruction with a generic model of process to which skeletal meiosis knowledge can be attached.

Constructing a complete and correct meiosis model is not nearly so easy, however, as is evidenced by the existence of individuals with alternate meiosis models at all three levels of expertise among the participants in this study. As opposed to the skeletal components of knowledge, more elaborated meiosis knowledge includes the many pieces of chromosome knowledge, event-specific and whole-process process knowledge, and knowledge about related biological phenomena (e.g., the existence of ordered tetrads)[22] that was either missing from alternate meiosis model participants' knowledge bases or about which they had misconceptions.

Knowledge base underlying the correct model of meiosis. Further specification of the model of constructing understanding is aided by brief consideration of the nature of a knowledge base underlying a correct model of meiosis. A knowledge base of this sort is illustrated in Figure 9. Pieces of skeletal knowledge are attached to the three components of generic process knowledge. More detailed pieces of chromosome, process, and stage knowledge exist as interconnected bundles attached to corresponding pieces of skeletal knowledge and each other. Knowledge about related biological phenomena is connected to appropriate pieces of more detailed knowledge. Constraints on how meiosis must proceed derive from connections between pieces of knowledge. For example, if replication occurs during S phase of the cell cycle (knowledge piece 1) and meiosis occurs just prior to cell division (knowledge piece 2), then replication must precede all other meiotic events (constraint imposed by connecting knowledge pieces 1 and 2), or if crossing over is the reciprocal exchange of pieces of individual chromosomes (knowledge piece 3) and physical proximity is a requirement for that exchange (knowledge piece 4), then

[22] Some organisms produce meiotic products in an elongated sac that holds them in the linear order specified by the preceding meiotic divisions. Any particular order is constrained by the relative order of the centromere, gene(s), and crossover events(s) that may have occurred during meiosis.

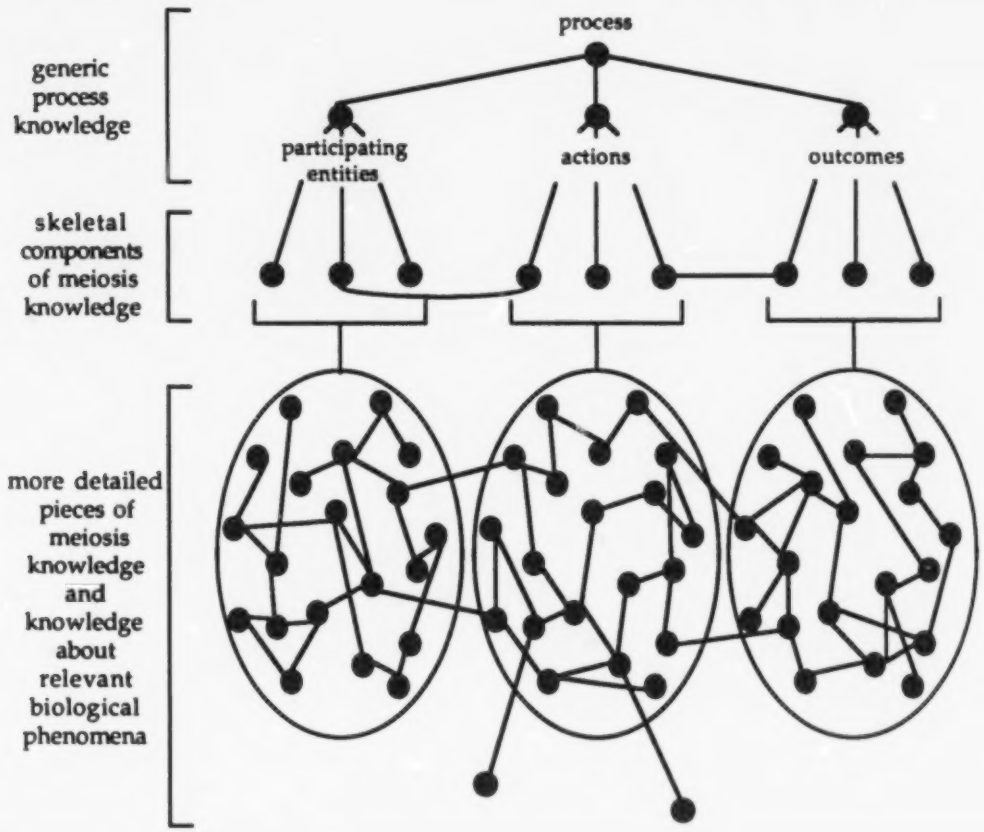

Figure 9. Schematic representation of the organization of a knowledge base underlying the correct meiosis model. Black dots represent individual pieces of knowledge and lines represent connections between pieces of knowledge. Circles surrounding groups of dots represent the organization of more detailed pieces of meiosis knowledge into bundles according to the three categories of skeletal knowledge: chromosomes, events, and stages. The two dots appearing below the 'actions' or 'meiotic events' bundle represent knowledge about two relevant biological phenomena.

pairing must precede crossing over (constraint imposed by connecting knowledge pieces 3 and 4). In its most complete specification, a knowledge base underlying the correct model of meiosis is complete, all pieces of knowledge are appropriately connected, and therefore, all constraints derived from these connections are mutually compatible.

Knowledge base underlying an initial model of meiosis. Turning now to constructing understanding, the following describes initial exposure to meiosis: introductory students (inexperienced novices) are rapidly exposed to many pieces of meiosis knowledge, presumably all the pieces necessary to formulate the correct meiosis model. As described earlier, some of these pieces, the skeletal components, are easily acquired and organized into a core conception of meiosis. Many, but not all, of the additional pieces are also picked up and loosely organized into the three bundles of more detailed knowledge. However, of the pieces present, some are appropriately connected to one another, some may be inappropriately connected to one another, and some are missing certain connections to other pieces of knowledge. In addition, some pieces of knowledge are missing. Thus, an inexperienced novice knowledge base (1) contains gaps and isolated clusters of knowledge and is missing certain constraints as a result of the absence of particular pieces of knowledge and connections, and (2) contains incorrect constraints if inappropriate connections are present.

A number of characteristics of the alternate meiosis models exposed by the inexperienced novices in this study support the model of constructing understanding following limited meiosis instruction. First, the intricacy of and the number of details specified in their meiosis models clearly demonstrates that, even after limited instruction, inexperienced novices have accumulated many pieces of more detailed meiosis knowledge. Individual instances of correct constraints, like pairing occurs between homologous chromosomes, point to the existence of some

correct connections between individual pieces of knowledge. However, the numerous deviations of the inexperienced novice alternate meiosis models from the correct overall meiosis model are indicative of knowledge bases in which pieces of knowledge were disconnected, inappropriately connected, and just plain missing.

The ploidy/structure chromosome misconception shared by several of the inexperienced novices can be explained as resulting from an inappropriate connection between the concepts of chromosome number and chromosome structure. This connection gives rise to the incorrect constraint that ploidy is a function of the number of DNA molecules present per individual chromosome. In addition to specific misconceptions like this one, the absence of anywhere from one to all of the three model qualities (completeness, stability, and internal consistency) among the inexperienced novices' alternate meiosis models can similarly be explained by the proposed model of constructing understanding (for more details, see Hildebrand, 1989) .

Changes with increasing expertise. The models of the two extreme knowledge bases, that of inexperienced novices and that which underlies the correct meiosis model, predict that three changes must occur in an individual's knowledge base as he or she develops expertise. First, additional pieces of knowledge must be added. Second, inappropriate connections between pieces of knowledge, if present, must be deleted. Third, appropriate connections between new and existing pieces of knowledge must be formed. Several aspects of the overall meiosis models and reasoning behaviors exhibited by the expert and experienced novice participants in this study support both the proposed model of knowledge organization underlying the correct model of meiosis and the above prediction of how an individual's knowledge base changes with increased expertise.

Although not all of the experienced novice and expert participants in this study exposed completely correct overall meiosis models, all of their meiosis models can

be distinguished from those exhibited by the inexperienced novices on two counts. First, while one experienced novice did display an alternate chromosome model, none of the expert and experienced novice participants harbored the ploidy/structure chromosome misconception shared by four of the five inexperienced novices. Second, in contrast to the inexperienced novice models, all 10 expert and experienced novice meiosis models included the three model qualities, completeness, stability, and internal consistency.

The first distinction points to the absence of a specific inappropriate connection, namely, the connection between the concepts of chromosome number and chromosome structure. The second distinction more generally addresses the presence of more pieces of knowledge and more connections in the knowledge base of an individual with greater expertise. The completeness of the models exposed by the more experienced participants suggests that they have accumulated more pieces of meiosis knowledge. The stability of these participants' models indicates that the knowledge bases underlying these models are relatively solid, a quality that would result from the existence of firm connections between many pieces of knowledge. This characteristic of a more expert knowledge base is also revealed by the internal consistency of these participants' models in that internal consistency would result from the presence of many mutually compatible constraints.

In addition to the features common to all expert and experienced novice meiosis models, the extent to which the five alternate models in this group deviated from the correct overall meiosis model also points to increasing numbers of pieces of knowledge and connections in the meiosis knowledge base with increasing expertise. With the exception of the meiosis model exposed by one experienced novice participant, the misconceptions in the expert and experienced novice alternate models were confined to one or two meiotic events. Further, most of these models could have been corrected by the addition of just a single piece of

knowledge. This suggests that the knowledge base underlying each of these alternate models was far more complete (i.e., it contained more accurate pieces of knowledge and more accurate connections between those pieces) than those underlying the inexperienced novices' alternate models.

The increase in the number of accurate pieces of knowledge and of accurate connections between those pieces in the knowledge base with increasing expertise was also revealed by certain reasoning behaviors displayed by some experts and experienced novices not reported earlier. Several experts and experienced novices explicitly utilized their knowledge of the biological phenomenon concerning the order in which gametes occur to solve for one or more of the gamete sets. This solution path required working backward through several steps of meiosis in order to specify crossover events necessary for a particular solution. This behavior points to the presence of knowledge of the biological phenomenon in the knowledge base, to its appropriate connection to other relevant pieces of knowledge, and to additional interconnections between appropriate pieces of knowledge that allowed for accurate backward chaining to a correct solution.

Finally, two participants who exposed the correct meiosis model displayed another reasoning behavior suggestive of the intricate interconnectedness of a knowledge base that underlies the correct meiosis model. Using diagrams of alignment I configurations, these two participants displayed the ability to reason directly between alignment I and the final products of a specific meiosis. Both could accurately explain the nature of the events occurring between alignment I and the final outcome of meiosis, but did not not show any evidence for appealing to that knowledge when reasoning. This indicates that in addition to having appropriately interconnected knowledge about the entire series of meiotic events, these participants also had compiled or 'short-cut' knowledge in the form of either a well

worn path between alignment I and final outcome knowledge or perhaps a direct connection between relevant aspects of these two knowledge clusters.

Transition mechanism--conflict resolution. The final issue to be addressed with regard to the model of constructing understanding is how the transition from an inexperienced novice knowledge base to one that underlies the correct meiosis model might occur. Two points made earlier concerning the nature of knowledge underlying the correct meiosis model bear on this issue. The first is that individual constraints derived from the underlying knowledge base interact with one another to give rise to the correct meiosis model. The second is that these constraints are mutually compatible, meaning that individual constraints do not conflict with one another.

In contrast to the correct meiosis model, I have described the knowledge bases underlying alternate meiosis models as being deficient in certain pieces of knowledge and connections between pieces of knowledge as well as containing certain inappropriate pieces of knowledge and connections between pieces of knowledge. The effects of missing and inappropriate knowledge/connections in a meiosis knowledge base would be the absence of particular constraints and the presence of incorrect constraints respectively. Because incorrect constraints are based on inappropriate knowledge or connections, these constraints will not be mutually compatible with other correct constraints. However, these constraints can function in the context of a knowledge base that is missing any constraints that might conflict with the incorrect constraints.

This characterization of the constraint structure underlying the correct and alternate meiosis models suggests a mechanism for the transition from a inexperienced novice knowledge base to one that underlies the correct meiosis model. This mechanism hinges on the recognition and resolution of conflict as pieces of knowledge accumulate and become connected in an individual's

knowledge base. For example, suppose an individual's current knowledge base gives rise to a meiosis model in which crossing over incorrectly occurs in each of the intermediate cells during meiosis II and knowledge of the biological phenomenon concerning the order in which gametes occur is added this knowledge base. The constraint that derives from this piece of knowledge being connected to knowledge about crossing over is that crossing over must occur in the initial cell during meiosis I. Thus, the new constraint conflicts with the conception of crossing over in the current model. If this conflict is recognized and the new constraint is accepted as valid, then the conflict can be resolved in the direction of the correct model. It is also possible that other components of the model could be changed to accommodate both the old, incorrect constraint and the occurrence of the biological phenomenon resulting in an even less correct model. A key question with regard to conflict resolution in the model of constructing understanding is, what determines the direction in which conflicts are resolved?.

In general, since constraints interact to give rise to an overall model of meiosis, a knowledge base underlying an alternate meiosis model that is close to being correct will be more constrained overall. Therefore, when conflict arises in the context of a nearly correct meiosis model, it is more likely to be resolved in the direction of the correct model. However, when conflict arises in the context of an alternate meiosis model that is missing constraints and/or contains other incorrect constraints, the direction of conflict resolution is much less certain. These points are exemplified by conflict resolution displayed by two experts with alternate meiosis models and two inexperienced novices in this study (not reported earlier).

Two of the expert participants who were apparently missing the piece of knowledge that replication is temporally separated from and occurs prior to meiosis, were uncertain as to whether replication occurred before or after crossing over. In both instances, they derived the constraint that replication must precede crossing

over from the fact that gamete set (iii) (see Figure 1) contained four allelic combinations of two genetically linked genes (a related biological phenomenon). In the context of their nearly correct meiosis models, their uncertainty (conflict) was resolved such that their proposed models were now functionally correct (i.e., their models specified the correct relative timing of replication and crossing over).

In contrast, one inexperienced novice who was also apparently missing the knowledge about the correct timing of replication was uncertain as to whether replication occurred before or after the first meiotic division. She also recognized the constraint imposed by the same biological phenomenon which in the context of her chromosome model required replication to occur before the first meiotic division. However, this constraint conflicted with her incorrect constraint that chromosome structure was a function of chromosome number. Because her knowledge base lacked other pieces of knowledge or connections that could have supported one or the other of these incompatible constraints, she left the conflict unresolved. Finally, conflict arose for another inexperienced novice concerning the number of individual chromosomes present in what she called haploid cells. Her incorrect constraint that chromosome structure was a function of chromosome number conflicted with her correct knowledge of the meaning of haploid with regard to chromosome number. In this case, the incorrect constraint apparently took priority over the correct knowledge, and she resolved the conflict in the direction of a more incorrect meiosis model.

Summary. A general picture of incorporating the many detailed pieces of meiosis knowledge into a meiosis knowledge base emerges from the preceding discussion and examples. In essence, constructing understanding beyond the core conception of meiosis involves the accumulation of pieces of relevant knowledge, the disassociation of inappropriate connections, and the establishment of appropriate connections through conflict resolution and accommodation of correct constraints.

The fact that even some experts exhibited alternate, albeit nearly correct, meiosis models indicates that this level of knowledge construction is far more demanding than construction at the skeletal level. This is hardly surprising given the number of and the intricate interconnection between the components that constitute this process.

Educational Implications

Although the model of constructing understanding of meiosis is somewhat speculative, several reasonably sound instructional implications can be derived from it. First, the description of the core conception of meiosis and its relation to generic process knowledge suggests that initial instruction should perhaps focus on those pieces of meiosis knowledge that most directly connect to generic process knowledge. This focus would encourage the construction of a sound core conception from which to build a more elaborate meiosis model. While the myriad of alternate meiosis models exposed in this study indicate that, (1) the core conception does not limit further knowledge accumulation to only those necessary and correct pieces of additional meiosis knowledge and (2) the core conception does not provide the degree of organization required to support a correct overall meiosis model, it certainly appears to serve as an organizing framework in initial model construction that is worth being exploited in instructional settings.

Possibly more important than making connections to generic process knowledge which appear to be established in even the faultiest of meiosis models is utilizing conflict resolution in teaching about meiosis. In the model of constructing understanding, conflict resolution occurs when an individual is actively engaged in reasoning about meiosis. It is in this context he/she becomes aware of incompatible constraints, the coexistence of which requires resolution ultimately leading to construction of the correct model of meiosis. Thus, I propose that reasoning about

meiosis plays a crucial role in constructing understanding of this process. Yet, in the context of standard meiosis instruction, students are provided with virtually no opportunities to reason about the process. Standard questions found at the end of textbook chapters on meiosis ask students to (1) compare and contrast mitosis and meiosis and (2) predict different gamete genotypes that can be derived from a described diploid cell undergoing meiosis (Ayala & Kiger, 1980; Curtis, 1983). The first activity basically involves redescription of the two processes focusing on similarities and differences and does not require consideration of how either process is constrained. The second activity can be approached algorithmically without directly appealing to knowledge of meiosis.[23] Another standard instructional activity through which it has been assumed students utilize their knowledge of meiosis is solving Mendelian genetics problems. However, research on Mendelian genetics problem solving has clearly demonstrated that students tend to solve these problems algorithmically as well and often are unaware of the connection between meiosis and solving Mendelian genetics problems (Peard, 1983; Stewart, 1982, 1983; Stewart & Dale, 1981; Tolman, 1982).

The inadequacy of these standard activities in promoting students' direct reasoning about meiosis reveals a need for the inclusion of new activities in genetics instruction that will foster this kind of reasoning. One obvious activity that could easily be incorporated into instruction is working on problems like the meiosis problem used in this research (see Figure 1). As a research tool, the meiosis problem elicited individuals' models of meiosis through their reasoning about the process for problem solving. Although constraint reasoning and conflict resolution were not a focus of the empirical analysis, it was pointed out in the previous description of the model of constructing understanding that several participants did

[23] Participants in this study solved a problem of this type as part of a "warm-up" exercise, and all did so algorithmically.

engage in these activities while working on this problem. Given that working on the meiosis problem occasionally triggered the spontaneous occurrence of these cognitive activities, it is likely that this problem could be modified in ways that would stimulate constraint reasoning and conflict resolution in instructional settings. Two example activities using this problem are described in the following paragraphs.

First, the meiosis problem could be presented in a form similar to that used in this study along with a follow-up question asking students to solve the problem again assuming that the four gamete genotypes resulting from a specific meiosis occurred in a particular order. I suggest the order of problem presentation, first without explicit consideration of the biological phenomenon followed by its inclusion, for the following reason. If inclusion of this biological phenomenon creates a constraint in the problem solver's knowledge base that is incompatible with the meiosis model he or she proposed initially, the subsequent introduction of the biological phenomenon sets up an obvious conflict that needs to be resolved. In addition to possibly prompting conflict resolution, the example problem could also contribute to the incorporation of knowledge about this biological phenomenon into the problem solver's knowledge base as well as the development of patterns of scientific thinking like, when building a model of a natural process, the model must account for observable phenomena associated with that process.

Another potential instructional activity using problems like the research problem involves having students analyze gamete sets for clues to specific problem solutions. For example, the occurrence of four different allelic combinations of two genes each heterozygous in the initial diploid cell ideally serves as a clue that crossing over is a component of the problem solution. This activity could assist students in becoming more aware of the constraints that define meiosis as well as encourage students to monitor their own reasoning processes. It would also be

useful to accompany any meiosis problem-solving activity with discussion about constraints and their role in defining the process of meiosis.

In addition to providing the context for conflict resolution, incorporating meiosis-reasoning problems into instruction is also advantageous in that (1) they encourage flexible thinking because individual gamete sets have more than one correct solution, (2) they force problem solvers to deal with the subtleties of crossing over, and (3) they afford problem solvers the opportunity to explicitly deal with the effects of a single cell versus a population of cells going through meiosis, the latter of which is far more common and often problematic with regard to the role played by probability (see Kindfield, 1990 for details).

Conclusions

The content and patterns of correct and mis- conceptions among participants at varying levels of expertise in genetics derived from the detailed microanalysis of individual reasoning about meiosis provided a basis for proposals concerning sources of misconceptions and a model of constructing understanding of meiosis. Potential instructional sources for many misconceptions and the model of constructing understanding suggest a variety of instructional changes that could assist students in developing more robust models of this crucial subcellular process. Chief among these changes are (1) to teach about nuclear division processes from a cell cycle perspective and (2) to provide students with opportunities for directly reasoning about the process of meiosis. If such changes are instituted, it is equally important that students be assessed in kind. Once again, the meiosis-reasoning problem utilized in this study can serve as a tool for uncovering the current state of students' understanding.

Another facet of instruction alluded to in discussion of the educational implications of the sources of particular misconceptions is the use of carefully

constructed and clearly defined diagrams. A major outcome of the larger study from which the results presented here were derived was the recognition that a robust understanding of meiosis includes a variety of pictorial skills that are virtually never addressed in instruction (Hildebrand, 1989; Kindfield, 1991). The more complete description of diagram-oriented-cell-cycle-based instruction found in Hildebrand (1989) integrates instructional changes suggested in this paper with instruction concerning pictorial aspects of understanding meiosis.

While the work presented here has focused on the process of meiosis, it seems a reasonable assumption that understanding meiosis is substantially similar to understanding other subcellular biological processes as well as other natural processes that involve nonarbitrary interactions between microscopic and submicroscopic entities. If so, the results of this work not only have implications for meiosis instruction, but are also applicable to instruction in a wide variety of subjects and domains like cellular physiology, organic chemistry, and subatomic physics.

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